Biology of the Thimbleberry Gallmaker *Diastrophus kincaidii* (Hymenoptera: Cynipidae)[1]

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The cynipid wasp, *Diastrophus kincaidii* Gillette, is a widely distributed species in western North America and is known to be the causative agent of a conspicuous gall of thimbleberry (*Rubus parviflorus* Nutt.). These galls, which are characteristic in form, may be extremely abundant on the host plant. Weld (1957) has reported that *R. parviflorus* is the only known host of *D. kincaidii*. According to Weld (in lit.), distribution extends from Los Gatos, California to British Columbia. Localities are listed for California, Oregon, Washington and Idaho. It is possible that *D. kincaidii* occurs outside of this range and its distribution may be coextensive with that of thimbleberry which extends from San Diego County, California north to Alaska and east into Idaho.

Little information on the biology of *D. kincaidii* has been reported in the literature, therefore a study was initiated to examine its life history and habits, its relationship to gall development and to establish its insect associates. The study was conducted in a redwood forest habitat east of Humboldt State University, Arcata, California, and supplemented with laboratory rearings from September 1970 to May 1973.

THE GALL

Mature galls on thimbleberry are abrupt swellings on the stem or petiole (Fig. 1). They are irregularly swollen or lumpy and glabrous. Their size and shape vary greatly depending on the number and precise location of cynipid larvae present in the gall. Larval cavities may be numerous and usually are situated closely together. The majority are located in the vascular zone but many extend into the pith and cortex as well. The tissue immediately surrounding each larval cavity is hard and woody as are the outer tissues of the gall but the tissue between cavities is loose and pithy. Each cavity is irregularly ovoid and about 2×3 mm in size.

Gall development proceeds rapidly following oviposition by the adult

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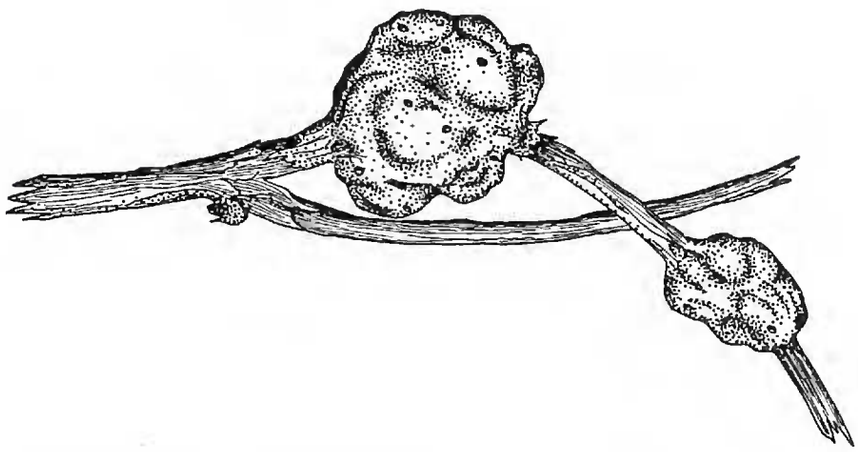

FIG. 1. Mature galls on thimbleberry, .5×.

female in the spring. First evidence is a slight swelling on a stem seven to ten days following egg deposition. The swelling is due to enlargement of cortical, xylem and phloem cells. At this stage of development larval cavities are not yet formed and the eggs and first instar larvae are wedged between plant cells.

In three to four weeks after oviposition larval cavities have developed and a gall is present as an abrupt and noticeable enlargement of the stem. The cavities are formed by a proliferation of parenchyma tissue that surrounds individual larvae. Xylem and phloem tissues of the gall are disrupted and only the uninfected portions of the stem have normal vascular tissue.

The tissues of most galls show signs of woodiness by the end of summer and during the fall all become woody.

DESCRIPTION OF LIFE STAGES

ADULT

Descriptions of the adult by Gillette (1893) and Fullaway (1911) will serve in the recognition of this species. The general characters are as follows: the female (Fig. 3a) ranges in size from 2.0 to 2.5 mm in length and the male is approximately 1.75 mm in length. The body is black. The antennae, tegulae and ovipositor sheath are brown to brownish. The legs are brown and the tips of the tarsi are black. The laterally compressed abdomen is larger in the female, approximately half the length of the body. The antennae are 13 segmented in the female and 14 segmented in the male.

EGG

The egg of *D. kincaidii* is readily recognized by its oblong shape and long stalk (Fig. 3b). Measurements of ten eggs averaged 0.65 mm (0.59–0.70) in length and 0.077 mm (0.052–0.104) in width. The stalk of the egg is approximately 1.3 × longer than the elongate oval body. The stalk is narrow along its length

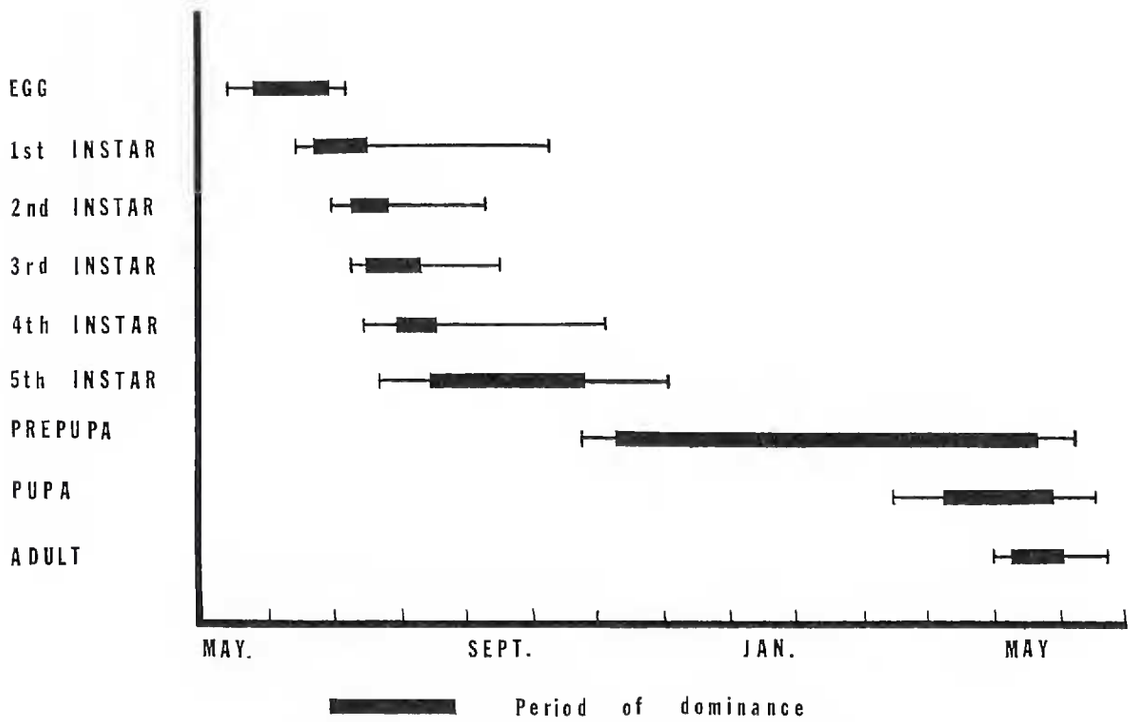

FIG. 2. Seasonal occurrence of life stages of *Diastrophus kincaidii*.

with a swelling at the distal end. The body is white and opaque and the stalk is clear. The chorion is smooth.

LARVA

This species has five larval instars that are similar in appearance (Fig. 3, c–e). The larvae range in size from 0.3 mm to 2.5 mm in the normal curved position. They are best distinguished by head capsule measurements (Fig. 4). The body is 13 segmented, white, translucent, tapering posteriorly, and is apodous. Waste products are visible and become darker with age and are confined to the center of the abdomen as an oval mass. The integument is smooth and lacks setae. The antennae are not visible. Mandibles are present but inconspicuous in the first instar. They are tridentate in the fifth instar (Fig. 3h).

PUPA

In *D. kincaidii* there is long-lasting prepupal stage in addition to a shorter pupal stage (Fig. 3, f–g). The prepupa is distinguished by the arcuate body and opaque yellowish color. The body is fatter than in larval stages so the head capsule is only about half the size of the prothoracic segment in lateral view. In older individuals the red pigment of the developing compound eyes is visible in the prothoracic segment and legs (not yet fully formed) can be seen beneath each thoracic segment. The mandibles of the larva are forced to the surface as the pupa develops and come to lie fully exposed on the face.

The free pupa is white to yellowish during early development becoming dark brown to black with age. The antennae and legs extend caudad and reach the abdomen. The overall shape is robust, especially in females. Pupae range in size from 2.0–2.5 mm.

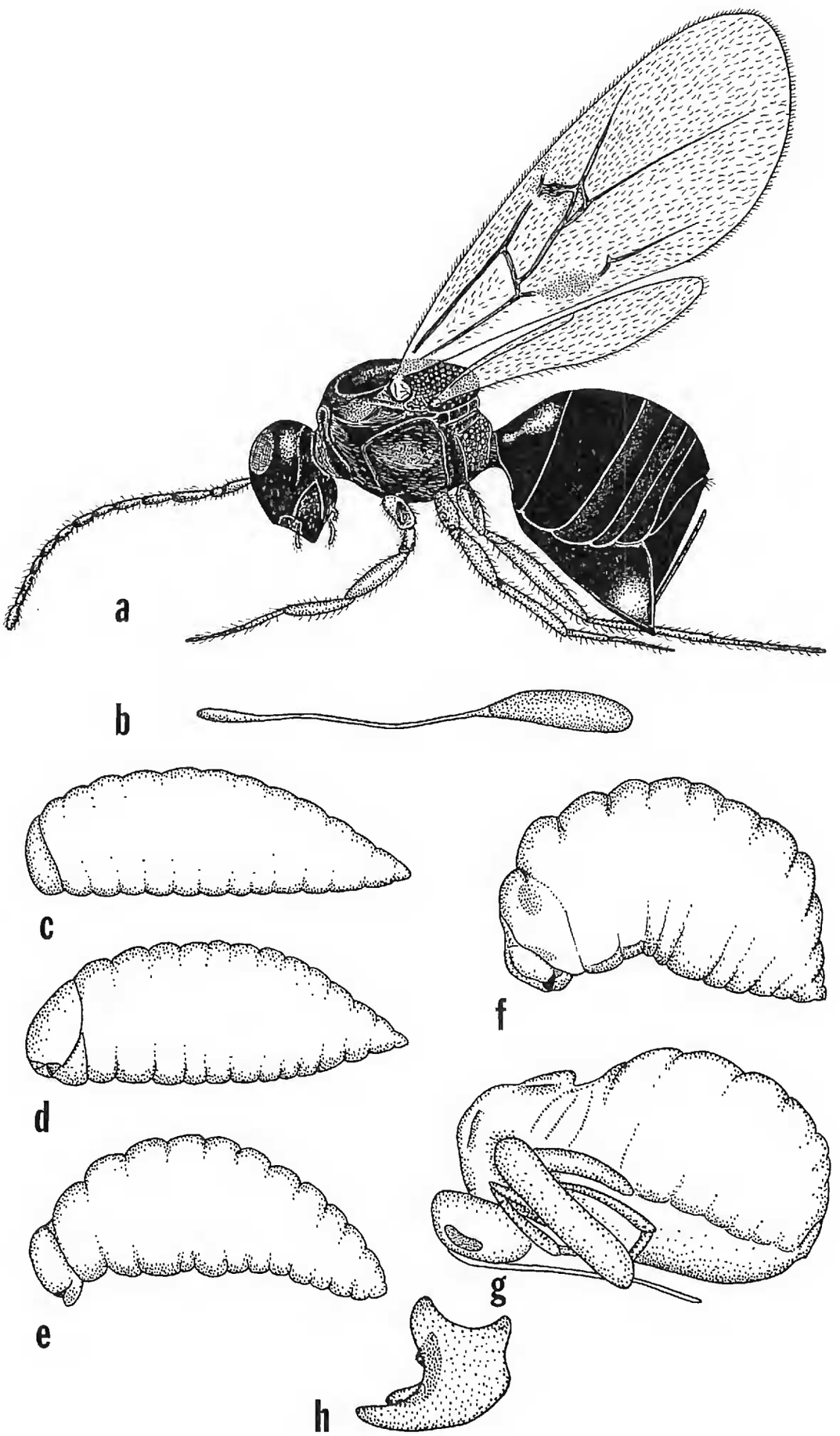

FIG. 3. Life stages of *D. kincaidii*. (a) adult, 22×, (b) egg, 68×, (c) 1st instar larva, 150×, (d) 2nd, 3rd and 4th instar larva, 90×–25×, (e) 5th instar

LIFE HISTORY

Diastrophus kincaidii is a univoltine species. The adults are relatively short lived following emergence in the spring. During the summer *D. kincaidii* passes through five larval instars and its galls become noticeable on thimbleberry. A long diapause begins as a prepupa in the fall and is broken the following spring when pupation occurs within the gall. The seasonsal occurrence of the life stages of *D. kincaidii* is summarized in Figure 2.

ADULT

Emergence. Adults emerge from galls in the spring and the emergence of all individuals within a gall is well synchronized. However, males emerge prior to females. Each adult chews through tissues of the gall to escape. The wings are fully expanded at this time. Chewing for the most part follows paths of least resistance and many adults work their way into the pith. Most adults fortuitously use exit holes created by others. Once the adult is free of the gall it is fully capable of moving about, but usually a few minutes are spent grooming or resting on the gall surface or adjacent stems. A striking characteristic of the adult is its unwillingness to fly. Neither males nor females were observed to fly in the field or laboratory. Generally, individuals wander over the surfaces of the host plant throughout adult life.

Courtship and Mating. Courtship, which occurs on various parts of the host plant, was observed many times in the laboratory and field. Upon encountering a female a male immediately shows excitement, hurriedly walks behind her and mounts from the rear without delay. In many instances males were observed to fan their wings once or twice prior to mounting. The female's response to these initial activities is always the same and is identical to her reaction to any other disturbance. Once touched by the male she crouches upon the stem or leaf so her venter touches or nearly touches the surface. Her head and antennae are held in contact with the surface and she remains motionless in this position.

The male caresses her thorax rapidly with his palps, usually touching the prothorax but sometimes caressing the mesonotum and scutellum. Simultaneously, his antennae move rapidly in front of her face, although

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larva, 17×, (f) prepupa, 13×, (g) pupa, 19×, (h) left mandible of 5th instar larva, 175×.

while she is in the crouched position they do not touch her. After three to five minutes the male may turn and touch her wings and/or abdomen with his palps; he then returns to his original position and continues caressing the thorax. It is common for the male to fan his wings at brief intervals during courtship.

The female usually remains motionless on the stem throughout the three to five minutes of courting until the male dismounts and walks away. The female then rises and continues to walk along the plant surface. Frequently the same male is attracted again and a second mating attempt may occur. It is also common for a female to simply drop from the plant to escape from the male.

After frequent encounters the female will begin to walk with a male in position for mating. He continues to court in the typical manner but with the female standing, their antennae touch. The antenna of the male alternately rubs the corresponding antenna of the female from the distal to proximal end. This movement is rapid and occurs while he continues to caress her thorax with his palps.

While the female is in the crouched position, the frequent attempts by the male to copulate are unsuccessful. Once the female is standing, however, the male is able to initiate copulation. This is accomplished when the male moves to one side of the female, grasps her wings and thorax with his forelegs and lowers himself alongside her abdomen. Their genitalia unite and mating occurs in this position.

Copulation lasts from thirty to sixty seconds. Both sexes are motionless during this period except for slight antennal movements and pulsating movements of the male's abdomen. Following copulation the male remains mounted on the female for a few seconds.

Males were often observed courting the same or different females following mating; however it is not certain that an individual male or female actually mates more than once. Males also commonly courted and attempted to mate with other males.

Oviposition. The time interval between insemination and oviposition is not known. In a single instance a female was observed to oviposit immediately after mating but the possibility of a prior mating could not be excluded in this case.

The search for a suitable oviposition site begins after the female has climbed up the stem to the current season's growth. She immediately begins an investigation of the green shoot axis and, occasionally, the petioles with her antennae. While she walks slowly and erratically over the stem, her antennae are moved up and down at a moderate rate, com-

ing very near the surface but touching it only occasionally. When a suitable site is located she stops and both antennae are held downward with the tips directed toward this site. The antennae quiver in this position for a few seconds, then the female steps forward, arches her abdomen and inserts her ovipositor. In so doing, the sternites are bent downward forming a "V" and the ovipositor is inserted in a smooth, continuous motion. In many instances females partially insert, pause, and then may withdraw the ovipositor. This apparent testing of the site may occur once or twice before the female locates a position on the stem suitable for oviposition. Once the ovipositor is fully extended and the venter touches the stem oviposition is accomplished.

During oviposition there are pumping movements of the lower abdomen while the female remains motionless, although the antennae and legs may sometimes quiver slightly. Testing of a site with the ovipositor lasts only a few seconds but actual oviposition lasts two or three minutes. Although the passage of eggs was never observed, a brown fluid was clearly seen passing into the plant tissue at the time of oviposition. This fluid occupies the entire path of the ovipositor in the plant tissues.

The ovipositor is withdrawn in a smooth motion and the female moves and reinserts it into the stem very near the previous ovipositional site. When a number of insertions have been made, brown wounds are visible on the plant surface. These wounds occur in clusters that range in size from 4–100 mm^2 and may be located on a side of the stem or may completely encircle it.

The number of eggs deposited by a female is not known, although it must exceed 30 to 50 as this is the number of larvae in an average sized gall.

The majority of the eggs are deposited in the xylem or phloem but a few are usually also located in the cortex or outer edges of the pith. Egg orientation does not appear to follow a regular pattern.

Oviposition was observed throughout the day. Such activity is greatest with sunshine and warm temperatures. An individual female may oviposit for an entire day and I believe in some instances into the following day. By the second day when oviposition is completed, the female leaves the oviposition site and moves to the tops of the plant. Females probably do not live very long following oviposition. In some instances individuals were found dead with the ovipositor still inserted in the plant.

A gall can result from the ovipositional activities of one female but it is not uncommon for two or three individual cynipids to oviposit in the same gall site. An individual will often oviposit in a second area

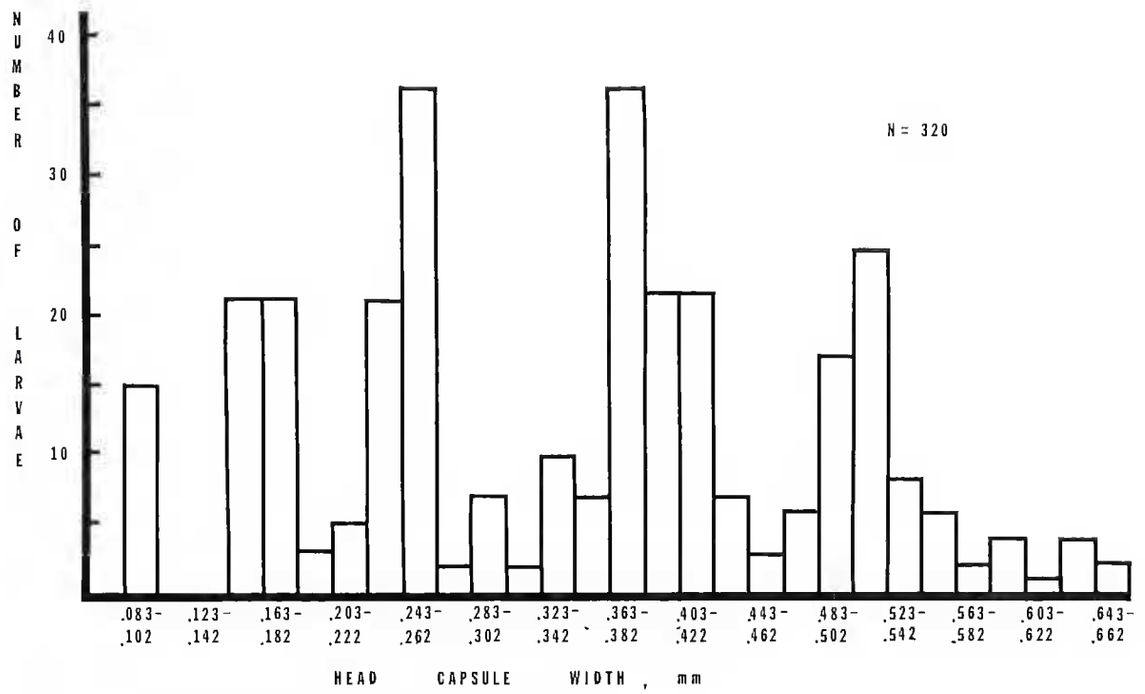

FIG. 4. Larval instars of *D. kincaidii*.

on the stem, usually above the first, but the galls which develop are consistently smaller and contain fewer larvae.

LARVA

First instar larvae are difficult to discern upon dissection of young galls. The larval cavities are not fully developed so there is little space between the larva and adjacent plant cells. The gall tissue is very wet and I believe that during the first instar ingestion of the surrounding fluid provides nourishment. The mandibles at this stage are barely detectable at 50 × magnification and movement of mouthparts cannot be seen.

By the time the second larval instar is attained, the larval cavities are well developed in a gall. The amount of parenchyma tissue surrounding the larva is extensive but the larva can move within the cavity it has made. Movement of the mandibles is now clearly visible. No changes in larval habits were observed from the second through the fourth instar.

During the fifth larval instar most galls become woody, to some extent. The fifth instar has larger, more heavily sclerotized mandibles which are adapted for chewing the dry tissues that line the larval cavity. These larvae are active within their cavities and move about to feed, thus their orientation in the cavity is not consistent. During feeding, it is common for a larva to chew through the tissue wall separating it

from an adjacent larval cavity. Apparently no harm is caused when two individuals occupy a common cavity because two pupae have been frequently found within one cavity in mature galls.

PUPA

Prior to pupation the characteristic coloration of mature larvae is an opaque yellowish due to the accumulation of extensive amounts of fat body. The development of pupal characters is gradual. Pigmentation of the eyes is most evident in older individuals and the outline of legs is only vague. *D. kincaidii* undergoes diapause during the winter in this prepupal stage. The prepupa is long lasting and one can expect to find galls containing prepupae 7 months out of the year.

By late April and May most individuals are in the pupal condition. In the laboratory the pupal condition lasted from one to two weeks at room temperature; in the field this period is probably longer. The development of the pupae within a gall is well synchronized with the others and the interval passed in this stage is relatively short.

INSECT ASSOCIATES

Ten species of parasitic hymenopterans were found associated with *D. kincaidii* on thimbleberry. Most are parasites of *D. kincaidii* but some are hyperparasites. Parasitism of *D. kincaidii* larvae is extensive during the summer and oftentimes only those individuals deepest within the gall tissue escape attack. The parasitic species emerge in succession throughout the summer and *D. kincaidii* is subject to parasitism for its entire larval life.

In addition, an inquilinous weevil and an undetermined cecidomyiid midge were occasionally present within galls.

The relationships of these species and the structure of the gall community will be discussed in a subsequent paper. The following is a listing of the insect associates inhabiting galls on thimbleberry.

Parasites—Ichneumonidae:	*Orthopelma californicum* Ash.
Torymidae:	*Torymus fagopirum* O. S.
	Torymus solitarius O. S.
Pteromalidae:	*Habrocytus* sp.
	Artholytus sp.
Eurytomidae:	*Eurytoma* n. sp. near *auriceps*
Eupelmidae:	*Eupelmella vesicularis* (Retz.)
Ormyridae:	*Ormyrus* sp.
Eulophidae:	*Tetrastichus* sp.

Inquiline—Curculionidae: *Rhynchites bicolor* (Fabr.)
Uncertain relationship—Cecidomyiidae: undetermined species

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LITERATURE CITED

FULLAWAY, D. J. 1911. Monograph of the gall-making Cynipidae of California. Ann. Entomol. Soc. Amer., 4: 331–381.

GILLETTE, C. P. 1893. Two new cynipids from Washington State. Can. Entomol., 25: 110–111.

WELD, L. H. 1957. Cynipid galls of the Pacific slope. Ann Arbor, Michigan. 80 pp.

BOOK NOTICE

THE BIOLOGY OF TRIBOLIUM WITH SPECIAL EMPHASIS ON GENETIC ASPECTS. A. SOKOLOFF. Oxford University Clarendon Press, Ely House, London W. 1. Volume 1. Pp. xix + 300, 22 tables and 76 figures in text. £12.00.

This is the first of 3 volumes which will form a study of the flour beetles of the genus *Tribolium*. Judging by this part they will also be an invaluable reference for workers on other genera and families of Coleoptera, and for students in other fields, since the coverage is monographic. The 8 chapter headings are: Introduction, Taxonomic position and evolutionary trends, Morphology, Internal anatomy and histology, Electron microscopy, Developmental and post-embryonic studies, Teratological abnormalities.

Each chapter is fully documented; the figures are nearly all compound (as many as 30 drawings), and the names of anatomical parts are fully spelled out. Keys include Hinton's on the genera of Ulomini of America north of Mexico and the species of adult *Tribolium* (with Sokoloff's summary of more recent findings), and to the pupae and mature larvae of *Tribolium* from Ho. Chapter 8 on teratological abnormalities, with illustrations of examples from the genus *Tribolium*, is a particularly useful summary and includes a 4-page tabulation of recorded abnormalities in the Coleoptera.—HUGH B. LEECH, *1435 Howell Mountain Road N., Angwin, California* 94508.